

A Review of the Genera of Oligositini (Hymenoptera: Trichogrammatidae) with a Preliminary Hypothesis of Phylogenetic Relationships

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Abstract.—The twelve genera of the tribe Oligositini (Trichogrammatidae: Oligositinae) are reviewed. The genus *Brachistagrapha* De Santis is removed from the tribe and synonymized with *Chaetogramma* Doult, a member of the Trichogrammatini (**new synonymy**). Phylogenetic analysis supports the recognition of two subtribes, the Oligositina and Eteroligositina. The large cosmopolitan genus *Oligosita* Walker is found to be polyphyletic and its current species are assignable to both subtribes. Those transferred to the Eteroligositina are now placed in the resurrected genus *Pseudoligosita* Girault, long considered a synonym of *Oligosita*. However, the removal of these species does not render *Oligosita* monophyletic. Remaining problems in the classification of the Oligositini are discussed. Included are a brief synopsis of each genus and a key to genera.

This study was prompted by an attempt to define *Oligosita* Walker, the most speciose genus of Trichogrammatidae. An examination of species soon suggested that two or more independent lineages existed within this common and cosmopolitan genus. Furthermore, it appeared that the tribe Oligositini could be divided into two broad phenetic groups of genera and that species in *Oligosita* were assignable to both. The apparent polyphyletic nature of *Oligosita* led to a review of the entire tribe. The results presented here include a preliminary phylogenetic analysis which tests our initial hypothesis of generic grouping, a generic key, and a brief taxonomic summary of each genus.

The current classification of Trichogrammatidae proposed by Viggiani (1971, 1984) is based largely on male genitalia. Two subfamilies are recognized, each with two tribes (Trichogrammatinae: Trichogrammatini, Paracentrobiini; Oligositinae: Chaetostrichini, Oligositini). The genitalia of Oligositinae are reduced and modified to form a single tubular structure which

lacks volsellae, parameres and a separate aedeagus (Fig. 10). The greatest modification occurs in the Oligositini where the anterodorsal aperture, the opening into which the ejaculatory duct enters, is extremely reduced in size (Fig. 11). Non-genitalic derived features supporting the monophyly of the tribe include black compound eyes and the single pair of setae on both the midlobe of the mesoscutum and the scutellum (Fig. 26).

The genera assigned to the Oligositini include *Chaetostrichella* Girault, *Doirania* Waterston, *Epoligosita* Girault, *Eteroligosita* Viggiani, *Hayatia* Viggiani, *Megaphragma* Timberlake, *Oligosita*, *Prestwichia* Lubbock, *Probrachista* Viggiani, *Prosoligosita* Hayat, *Pseudoligosita* Girault and *Sinepalpigramma* Viggiani and Pinto. *Pseudoligosita*, long treated as a junior synonym of *Oligosita* (Doult and Viggiani 1968), is resurrected to house species removed from *Oligosita*.

The monotypic genus *Brachistagrapha* De Santis (1997), although considered related to *Chaetostrichella* when described is not an oligositine. We have examined the

holotype and paratype of *B. caudata* De Santis and find that the species belongs to the genus *Chaetogramma* Doult (Trichogrammatini). It is very close to described species. We therefore treat *Brachistagrapha* as a junior synonym of *Chaetogramma* (New synonymy).

PHYLOGENETIC ANALYSIS

Taxa.—Phylogenetic analysis treats 15 oligositine OTUs. Included are *Chaetostri-chella*, *Doirania*, *Epoligosita* (*Epoligosita*), *Epoligosita* (*Epoligositina*) Livingstone and Yacoob, *Eteroligosita*, *Hayatia*, *Megaphragma*, *Prestwichia*, *Prosoligosita*, *Pseudoligosita* and *Sinepalpigramma*. A single undescribed species of *Pseudoligosita*, sp. I, from Israel, is analyzed separately. Also separated are three groups of species which remain in *Oligosita*: *Oligosita*-C (= the Collina Group as defined by Nowicki 1936, and Viggiani 1976b), *Oligosita*-M (= the Minima Group as defined by Nowicki 1936, and Viggiani 1987), and a group of generalized *Oligosita* which differs from congeners in certain characters used in analysis but does not belong to either of the other assemblages (= *Oligosita*-G). With the exception of *Oligosita*-G, *Oligosita*-M and *Pseudoligosita* (see below), all groups analyzed are confidently hypothesized as monophyletic based on morphological synapomorphies. Characteristics of all assemblages and an indication of material studied are given in the generic synopses.

The oligositine genus *Probrachista* was excluded from analysis. It is known from females only, and the few specimens available are slide mounted precluding adequate examination of several features. *Pseudoligosita gerlingi* (Viggiani), a species differing considerably from congeners, also was excluded because of inadequate material (see below). In addition, we did not consider a small group of undescribed *Pseudoligosita* which are likely to be assigned to *Doirania* once males are discovered (also see below).

The genus *Uscana* is used as the out-group for phylogenetic analysis. It was selected for the following reasons: 1) It is a generalized representative of the Chaetostri-chini, the other tribe of Oligositinae. 2) The structure of its male genitalia deviates minimally from that of the Oligositini; the primary difference is the larger anterodorsal aperture (Fig. 10, also see Viggiani 1971). 3) Its antenna has four postanellar flagellomeres (Fig. 15), the maximum number found in the Oligositini. The inclusion of *Bloodiella* Nowicki, a chaetostri-chine with antennal segment number and arrangement similar to most oligositines (see Doult and Viggiani 1968), was precluded because of insufficient study material.

Characters.—Thirty-two binary and multistate morphological characters were coded for analysis; all were treated as unweighted and unordered. Autapomorphies associated with binary characters were not included, the exception being those characterizing the entire tribe (chars. 2, 4, 6, 28). Character selection focused largely on features without intragroup variation. All but two of the characters (chars. 9, 20) coded below are invariable within all OTUs. These two are entered as polymorphic.

The following characters were employed for analysis. The character matrix used is given in Table 1.

1. Distance from toruli to epistomal suture: subequal to clypeus length (0); distinctly greater than length of clypeus (1). The position of the toruli varies considerably in the family. In most genera they are in the more ventral position.

2. Eye color: reddish (0); black (1). Eye color is reddish in virtually all Trichogrammatidae; black eyes distinguish the Oligositini.

3. Funicular segment of antenna: distinctly separated from club segments (0) (Fig. 16); approximating club base, resulting in club appearing 4-segmented (1) (Fig. 20). Separating funicular from club

Table 1. Data matrix for the 32 characters used in the phylogenetic analysis. Polymorphisms indicated by letter 'a' (= 0/1).

Taxon	Characters																																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32					
<i>Uscana</i>	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0		
<i>Megaphragma</i>	1	1	0	1	1	1	1	1	1	0	0	0	0	3	0	0	1	1	0	1	1	3	0	0	1	0	0	1	0	0	1	0	0	0	0		
<i>Prestwichia</i>	1	1	1	1	1	1	1	1	1	0	0	0	0	3	0	1	1	1	0	1	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0		
<i>Sinpalpigramma</i>	1	1	1	2	1	1	0	1	0	1	0	1	0	0	2	0	1	1	0	1	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0		
<i>E. (Epoligosita)</i>	0	1	0	1	0	1	1	1	0	1	1	0	0	2	2	1	0	1	1	0	1	3	1	0	0	0	0	1	0	0	0	0	0	0	0		
<i>E. (Epoligositina)</i>	0	1	0	1	0	1	1	1	0	1	1	0	?	3	2	0	0	1	1	1	1	3	1	0	0	0	0	1	0	0	0	0	0	0	0		
<i>Oligosita</i> - M	1	1	0	1	0	1	1	1	0	0	1	0	0	2	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0		
<i>Oligosita</i> - C	0	1	0	1	0	1	1	1	0	0	1	0	0	2	1	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
<i>Oligosita</i> - G	1	1	0	1	0	1	1	1	0	0	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
<i>Pseudoligosita</i>	0	1	0	1	0	1	0	0	a	0	1	1	1	1	0	1	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0		
<i>Pseudoligosita</i> - 1	0	1	0	1	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0	0	1	1	0	0
<i>Prosoligosita</i>	1	1	1	1	0	1	1	1	0	0	1	0	?	2	1	1	1	1	0	a	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
<i>Doirania</i>	0	1	0	1	0	1	0	0	1	0	1	1	1	1	0	1	0	0	0	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	
<i>Chaetostriarella</i>	0	1	0	1	0	1	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	
<i>Hayatia</i>	0	1	0	1	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	2	2	1	2	0	1	1	1	1	1	
<i>Eteroligosita</i>	0	1	0	1	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	2	2	1	2	0	1	1	1	1	1	

segments often is arbitrary in chalcidoids. In most oligositines the single funicular segment is distinctly separated from the club. In some members of the tribe, as in *Uscana* (Fig. 15), it approaches the club rather closely. The difference between antennal structure in *Prosoligosita* (defined as having a 4-segmented club) and *Prestwichia* (with 1 funicular segment closely appressed to its 3-segmented club) is minimal. Deciding between the two character states as defined here, however, is relatively straightforward. Although there also is variation in antennal segment number in the tribe it was not incorporated into the analysis because of considerable intrageneric plasticity (e.g. in *Megaphragma* and *Epoligosita*).

4. Placoid sensilla on second postantennal segment of female: present (0) (Fig. 15); absent (1) (Figs. 16–18, 20, 22). The absence of placoid sensilla on this segment characterizes females of all Oligositini. They are present in the outgroup and in several other genera.

5. Maxillary palp: present, well developed (0) (Fig. 23); present but reduced in size (1); absent (2) (Fig. 24). The maxillary palp in most Trichogrammatidae (state '0')

consists of 1 or 2 distinct segments with 2–3 apical sensilla. In state '1' at least 1 terminal sensillum remains but the segment is reduced considerably in size.

6. Pairs of setae on the midlobe of the mesoscutum and scutellum: two (0), one (1). A single pair of setae on both the mesoscutal midlobe and scutellum characterizes all oligositine genera. Two pair on each is typical of most other trichogrammatid genera. In a few genera (e.g. *Pintoa*) there is a single pair on the midlobe but 2 pair on the scutellum.

7. Propodeal disk: not well differentiated, short, straplike, at most slightly produced posteriorly with an arcuate posterior margin, not distinctly longer than metanotum (0) (Fig. 29); distinct, produced posteriorly, often triangular or rectangular, distinctly longer than metanotum (1) (Figs. 26–28).

8. Propodeal and mesopleural surface: relatively smooth (0) (Fig. 31); subrugose or subrugulose (1) (Fig. 30). This character refers to the surface of the entire mesosoma but is best contrasted on the propodeum and pleural areas. In *Sinpalpigramma* (scored as '1') only the pleural areas are subrugose.

9. Propodeal spiracle: an anterior slit between spiracle and anterior margin of propodeum present (0); an anterior slit absent, propodeal spiracle surrounded by cuticle (1). It appears that an anterior slit occurs in most trichogrammatids. This feature is sometimes difficult to code because instead of a deep slit there is only a groove anterior to the spiracle. The distinction between '0' and '1' is especially problematic in slide mounted material. Both states occur in *Pseudoligosita*.

10. Subpropodeal lobe: absent (0); present (1) (Fig. 25). In *Epiligosita* (*Epiligosita*) and apparently *E. (Epiligositina)* there is a small auricular lobe subtending the propodeal disk. It is not clear if this structure is propodeal or associated with the first metasomal segment. We are not aware of this structure in any other trichogrammatid. Although best appreciated with the SEM, on well cleared slide-mounted specimens this lobe appears as a small triangle immediately behind the propodeal disk. The presence of this structure has been verified in numerous nominate *Epiligosita*. Our representation of *Epiligositina* is scanty (2 specimens), and the consistent presence of a lobe in this subgenus remains questionable.

11. Mesophragma: evenly rounded, entire apically (0); bilobed apically (1). The apex of the mesophragma is apically bilobed in most trichogrammatid genera.

12. Mesopleural suture: present (0) (Fig. 30); absent (1) (Fig. 31). This character is not easy to appreciate in card- or slide-mounted specimens. In addition to the difficulty attributable to body size, the presence of an internal pleural ridge can be misinterpreted as a pleural suture. In several taxa a distinct line, appearing to be the pleural suture, extends from the base of the mesocoxa to the fore wing base. SEM examination however showed no external evidence of a suture in these specimens. A pleural suture, evidenced by a distinct external line or groove, characterizes most genera of trichogrammatids.

13. Mesosternum: without transepisternal sulci (0) (Fig. 32); with transepisternal sulci (1) (Fig. 33). In the Oligositini the presence of transepisternal sulci (*sensu* Gibson 1989) is correlated with the absence of the mesopleural suture. However, presence or absence of these sulci are included here as distinct from character 12 because the correlation does not occur in all trichogrammatid genera (e.g. in *Lathroueroidea* [unpubl. obs.]). We are not yet aware of transepisternal sulci in any non-oligositine taxon of Trichogrammatidae.

14. Maximum fringe length of fore wing to greatest fore wing width: 0.2 or less (0); 0.3–0.7 (1); 0.9–1.5 (2); >2.0 (3). This character was coded after recording the fringe/wing width ratio for a range of representatives of each OTU. Although there is a general difference in fringe length among taxa it is almost certain that the gaps between codes would be bridged with additional sampling. Because fringe length is roughly correlated with wing width (see Figs. 2–7), the latter was not employed as a separate character.

15. Fore wing disk setation density: dense to moderately dense (0) (Figs. 4–7); relatively sparse (1) (Fig. 3); without setae on disk (2) (Fig. 2). This character was quantified for exemplars of each OTU as follows: across widest aspect of wing, distance in mm taken between 4–6 setae from anterior to posterior margin of wing and the mean distance calculated; distances were measured from a seta to the nearest seta posteriorly. If no closest seta existed posteriorly or setation consisted of only a single row of setae (e.g. *Megaphragma*), then distance taken to wing margin(s). For state '0', intersetal distance ranged from 0.008–0.016 mm; for state '1', it ranged from 0.023–0.029 mm.

16. Basal sensilla on fore wing (immediately anterior to retinaculum on dorsal surface): absent (0); present (1). These refer to the presence of a small field of minute unsocketed structures at the base of the wing (illustrated in Pinto 2004). In some

taxa (e.g. *Oligosita-C*) they are acuminate apically; in others (e.g. *Pseudoligosita*) they commonly are clavate. Although these structures also occur in certain non-oligositines (e.g. the Paracentrobiini), they appear to be absent in the majority of genera, including the more primitive groups (i.e. members of the Trichogrammatini).

17. Posterior margin of fore wing: without an abrupt shift in outline at apex of retinaculum (0) (Fig. 3); with an abrupt shift in outline immediately beyond apex of retinaculum, resulting in wing width being slightly narrower at this point than at apex of retinaculum itself (1) (Fig. 4). Although state '1' seems to be associated with narrow wings the correlation is not perfect by any means. For example, several taxa with quite narrow wings (e.g. *Epoligosita*, *Oligosita-C*) are exceptions.

18. Premarginal vein with apical seta: present (0); absent (1). A basal and apical seta occur on the premarginal vein in most Trichogrammatidae.

19. Premarginal vein at junction with marginal vein: of similar width to marginal vein (0) (Figs. 3–7); abruptly wider than marginal vein (1) (Fig. 2).

20. Number of campaniform sensilla at apex of premarginal vein: two (0); one (1). Two campaniform sensilla mark the apex of the premarginal vein in trichogrammatids. In some taxa only a single sensillum is obvious. This reduction tends to be more common in groups with smaller body size. *Prosoligosita* possesses either 1 or 2 sensilla.

21. Stigma: subtriangular or subrectangular, connected to marginal vein with a distinct and narrow stigmal vein (0); subcircular or suboval, sessile to marginal vein or connected by a slight constriction only (1).

22. Number of rows of setae on disk of hind wing: three (0); two (1); one (2); zero (without setae) (3). The more primitive groups of Trichogrammatidae tend to have more dense hind wing setation. Al-

though roughly related to wing width, this correlation has several exceptions.

23. Mesotarsus: shorter than mesotibia (0); distinctly longer than mesotibia (1).

24. Metasomal terga: surface of all more or less similar entire length (0); at least the anterior-most 3 with posterior section (half or more) striate, with longitudinal cuticular stripes contrasting with evenly sclerotized anterior section of tergum (1) (Figs. 29, 31). The striations characterizing state '1' are usually distinct and easily seen. However in some species they are exceedingly faint and visible only under high magnification of well-cleared specimens, or with SEM. The anterior-most sternum may be longitudinally striate as well. Bipartite metasomal terga and sternum are unknown outside of the Oligositini.

25. Metasomal tergum VII: with spiracles (0); without spiracles (1). The absence of spiracles on the 7th metasomal tergum is an uncommon feature in trichogrammatids. We are aware of this trait only in the Oligositini.

26. Metasomal tergum VII in males: not noticeably modified (0); darker than preceding terga and presumably with a thicker cuticle (Fig. 13), surface sometimes modified as well (asperous or subrugulose) (1); with a small reticulate patch anteromedially (2). It is not clear how state '2' relates to state '1' except that it represents a modification of the same tergum.

27. Metasomal venter of male: normal, without medial projections (0); with a single posteriorly directed projection (1) (Fig. 35); with 2 or 3 narrow medial projections (2). States '1' and '2' represent unique features in the Trichogrammatidae. In state '1' there is a single projection. The structure is subquadrate in *Doirania leafsmanni* Waterston (see Pinto 2004). It is elongate and linguiform in *Pseudoligosita* and *Chaetotrachelia* (Fig. 35) and apparently also in *Doirania elegans* Pinto although shriveling of the single male available for SEM preparation precludes adequate description. In *Pseudoligosita* at least, the medial projec-

tion appears to be an extension of sternum IV (Figs. 13, 35). It is poorly sclerotized and visible but difficult to discern in slide-mounted specimens. In state '2' there are at least 2 very narrow, elongate medial sternal projections. Viggiani (1976b: Tbl. II, Fig. 4) shows three in *Eteroligosita tamaricis* Viggiani. We observe at least 2 in *Hayatia*. The anteriormost projection in state '2' is presumably homologous to that in state '1'. The function of these unique structures is unknown.

28. Male genitalia: with relatively large anterodorsal aperture (0) (Fig. 10); with reduced anterodorsal aperture (1) (Figs. 11, 12, 36, 37). The reduced anterodorsal aperture is a defining feature of the Oligositini.

29. Male genitalia: a simple tube with, at most, 2 longitudinal, anteriorly directed apodemes at base (0) (Fig. 11); variously modified at apex but with 2 posteriorly directed apodemes (1) (Figs. 12, 36); of a highly modified type (2).

As indicated, the male genitalia in the Oligositinae are considerably reduced and modified relative to the generalized chalcidoid condition. In the Chaetostrichini all genitalic parts are consolidated into a single tube but a relatively large anterodorsal aperture remains (Fig. 10). In the Oligositina and in at least *Doirania* as well as a few species of *Pseudoligosita* of the Eteroligositina (state '0'), this condition is retained except the aperture becomes considerably reduced with some basal sclerotization associated with the rim of the aperture remaining (Fig. 11). State '1' represents a modification primarily of basal structure. The anterodorsal aperture opens anteriorly instead of dorsally and the sclerotization surrounding the aperture has 2 elongate, posteriorly directed arms or apodemes which subtend the shaft of the genitalia and are attached to the sternal plate beneath (apparently sternum VII, see Figs. 14, 36, 37). These apodemes also may continue anteriorly a short distance. The genitalia are strongly

arched dorsally as is the sternal plate beneath (Figs. 14, 37). During genital exertion the base of the genitalia does not move relative to its sternum. Instead the strongly arched sternum beneath is flattened out which, owing to its attachment to the genital base, swings the strongly curved genital shaft ventrally and out of the body between divided sternal plates. The mechanism causing genital exertion is unknown but the genitalia can easily be forced out in specimens softened in alcoholic KOH by gently squeezing the metasoma, suggesting that hydrostatic pressure may be involved.

The genitalia in state '0' also appear to be stationary at the base. In state '0' taxa the genitalia also exit the body between the strongly incised (or completely divided?) last sternum (Fig. 34). The genitalia of *Pseudoligosita* I may represent an intermediate condition between states '0' and '1'. The posteriorly directed apodemes, while apparently present, are very short, and the genitalia are not strongly curved. Sternal modifications also are absent in this species.

Whereas states '0' and '1' represent relatively straightforward modifications of the generalized chaetostrichine genitalia, state '2', characterizing *Hayatia* and *Eteroligosita*, is not so easily understood. In these genera the genitalia are modified into an exceptionally elongate serpentine structure (Fig. 38), which is folded upon itself when at rest within the metasoma (Fig. 39). The anterodorsal aperture is very small but its orientation is not clear (see Viggiani 1976a).

30. Male genitalia: slightly curved ventrally (0) (Figs. 11, 34); strongly curved ventrally (1) (Figs. 12–14, 37).

31. Genitalia entire at apex (0) (Fig. 34); bifid at apex (1). The apex of the genitalia (= aedeagus) in *Pseudoligosita*, *Chaetostrichella*, *Hayatia* and *Eteroligosita* is bifid, however in the former 2 genera it is only slightly so (Fig. 36) compared to the condition in *Hayatia* and *Eteroligosita* (Fig. 38).

Table 2. List of synapomorphies for clades in Figure 1.

Clade	Defining synapomorphies ¹
A. Oligositini	2, 4, 6, 16 ² , 22 ³ , 28
B. Eteroligositina	8, 12, 13, 24
C. (<i>Pseudoligosita</i> - <i>Chaetostrichella</i>)	9, 26, 27, 29, 30, 31
D. (<i>Hayatia</i> - <i>Eteroligosita</i>)	26 (0-2), 27 (0-2), 29 (0-2), 31, 32
E. Oligositina	7, 14, 21
F. (<i>Oligosita</i> C - <i>Prestwichia</i>)	14 (1-2), 15 ⁴
G. (<i>Epoligosita</i> - <i>Prestwichia</i>)	18
H. (<i>Epoligosita</i> - E. [<i>Epoligositina</i>])	10, 15 (1-2), 19, 22 (1-2), 23
I. (<i>Oligosita</i> M - <i>Prestwichia</i>)	1, 17, 20
J. (<i>Prosoligosita</i> - <i>Prestwichia</i>)	3 ⁵
K. (<i>Sinepalpigramma</i> - <i>Prestwichia</i>)	5, 9, 15 (1-0), 25
L. (<i>Megaphragma</i> - <i>Prestwichia</i>)	11, 14 (2-3)

¹ Characters listed assume advance from 0 to 1 unless indicated in parentheses. Character explanations given in text.

² Reversed in *E. (Epoligositina)* and *Megaphragma*.

³ Reversed in *Hayatia*.

⁴ Reversed in clade K.

⁵ Reversed in *Megaphragma*.

32. Third valvulae of ovipositor: normal in width, not abruptly narrower than 2nd valvulifer (inner plates) (0); abruptly narrower than apex of 2nd valvulae, bristle-like (1) (see Viggiani 1996).

Analysis.—Phylogenetic analysis of the Oligositini employed maximum parsimony using PAUP* 4.0b10 (Swofford 2002). The branch and bound tree-searching algorithm was employed. Unweighted analysis was followed by successive approximations character weighting (Farris 1969) using the rescaled consistency index (maximum value) and a base weight of 1000. Summary statistics represent values after characters were reweighted at unity following successive approximations. Results were compared by generating strict consensus cladograms following both unweighted and weighted runs. Selected cladograms were transported to MacClade 4.0 (Maddison and Maddison 2003) for character analysis. Bootstrap values (nreps = 1000) were calculated to show level of clade support.

Results.—Branch and bound analysis resulted in five trees of 59 steps (CI = 0.70; RI = 0.82). Successive approximations weighting produced four trees with the

same tree statistics. The strict consensus tree from the weighted analysis is presented in Fig. 1. This consensus tree is the same as that produced by unweighted analysis except for the relationship between *Pseudoligosita* and *Chaetostrichella*. Successive approximations hypothesizes a sister group relationship, whereas unweighted analysis leaves their relationship within the *Doirania-Eteroligosita* clade unresolved.

Table 2 lists the synapomorphies for the various clades (A–L) indicated in Fig. 1. Analysis justifies dividing the tribe into two subtribes, the Oligositina and the Eteroligositina. The tribe Oligositini (clade A) is supported by several derived features. There also is robust support for distinguishing the Eteroligositina (clade B) from remaining members of the tribe. The three features supporting the Oligositina (clade E) are somewhat subjective, quantitative and difficult to code. The monophyly of this subtribe remains questionable, relatively high bootstrap support notwithstanding. Although more convincingly monophyletic, relationships are poorly resolved within the Eteroligositina

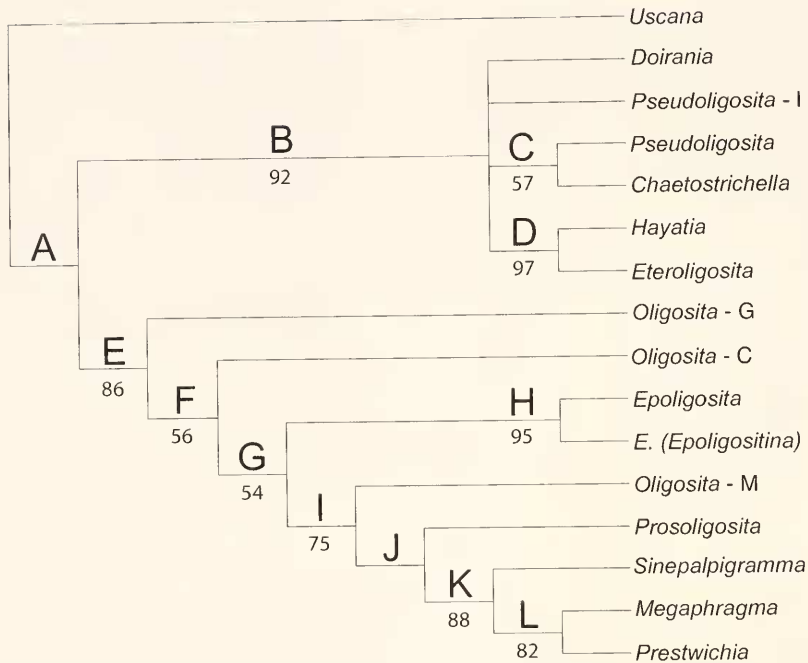


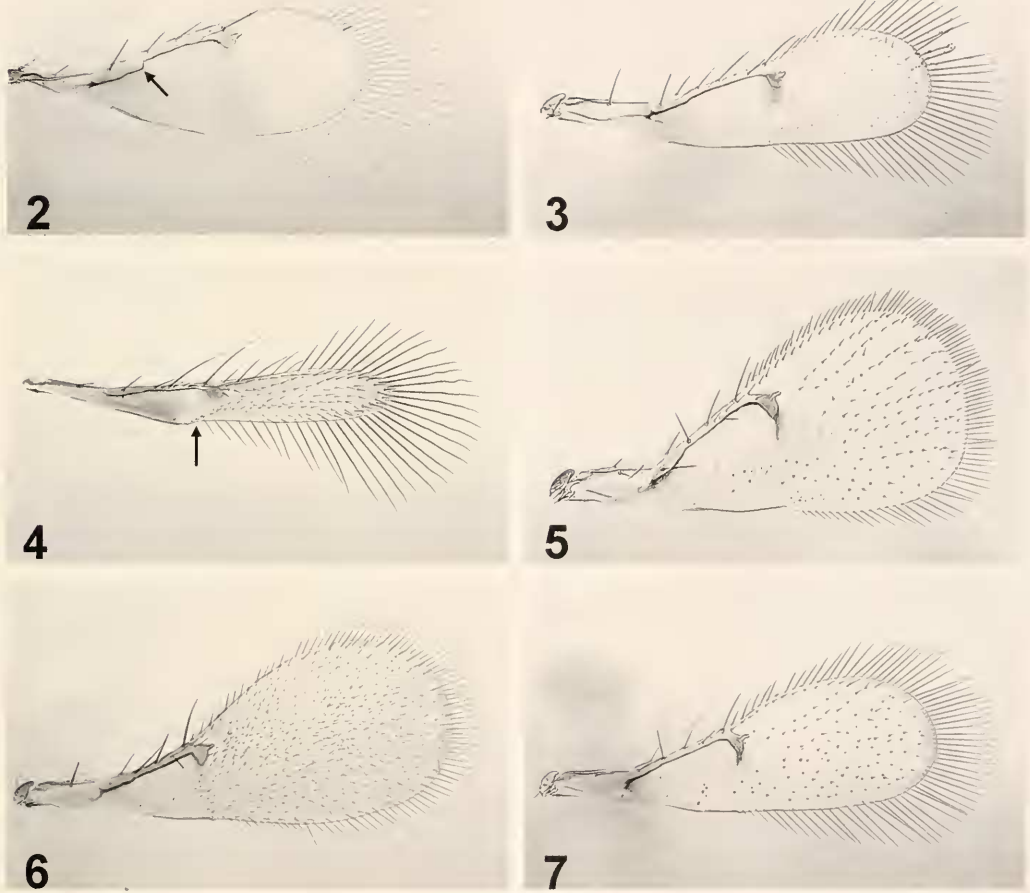
Fig. 1. Strict consensus of four cladograms after successive approximations weighting based on character data in Table 1. Tree length = 59; consistency index = 0.70; retention index = 0.82. Bootstrap values (if > 50%) are placed below the branches. Synapomorphic characters for clades A–L given in Table 2. The unweighted consensus tree (same statistics) differs only in that the sister group relationship between *Pseudoligosita* and *Chaetostrichella* (clade C) is not supported.

(clade B). The sister group relationship between *Hayatia* and *Eteroligosita* (clade D) has considerable support, but other relationships require additional input and taxon sampling. *Pseudoligosita* and *Chaetostrichella* are likely closely related (clade C). We are aware of no derived features defining *Pseudoligosita* not also shared with *Chaetostrichella* and it is possible that the latter simply represents a derived element of *Pseudoligosita*. Given the lack of derived features, *Pseudoligosita*-I is not given generic status at this time. *Probrachista* was not available for analysis but it clearly belongs to the Eteroligositina and appears closest to *Chaetostrichella* (see below).

Although the Oligositina is questionably monophyletic, there is strong support for two clades within the subtribe. Clade H [(*Epoligosita*-*E. (Epoligositina)*)] is defined by several characters and is compatible with treatment of the two taxa as conge-

neric. Clade K is based on four characters including the loss of the posterior metasomal spiracles, as far as we know, a unique feature in the family. Most of the remaining clades are questionable and require testing by additional evidence particularly since several of the apomorphic features represent reductions and perhaps are correlated with small body size. Figure 1 shows that *Oligosita* as herein defined remains polyphyletic even with the removal of *Pseudoligosita*.

Discussion.—The preliminary nature of this study prevents us from making all taxonomic changes suggested by the results. We consider the primary purposes of our analysis to be providing an estimate of the coarse phylogenetic topology of the tribe and determining if our initial hypothesis of *Oligosita* polyphyly could be supported. We believe the value of phylogenetic analysis as not only justifying



Figs. 2-7. Fore wings of Oligositini genera. 2, *Epoligosita* (arrow to abruptly wider premarginal vein). 3, *Oligosita*-C species. 4, *Prestwichia* (arrow to abruptly narrower margin of wing apical to retinaculum). 5, *Eleroligosita*. 6, *Probrachlusa*. 7, *Pseudoligosita*.

taxonomic modification but also as identifying problems requiring additional input before taxonomic resolution. Thus, we feel the character evidence is adequate to support dividing the Oligositini into two subtribes and removing several *Oligosita* and placing them in a resurrected *Pseudoligosita* belonging to the other subtribe. However, we hesitate dividing *Oligosita* further, notwithstanding its continued depiction as polyphyletic. This is an enormously diverse and character-poor genus. Perhaps the majority of species await discovery and description. At least one of the

subgroups incorporated in the study (*Oligosita*-G) is a heterogeneous assemblage without well-defined features. Also, all implied relationships involving sections of *Oligosita* in Figure 1 either have minimal character support, and/or are based on character loss or qualitative traits especially prone to subjective coding (Table 2). This also is reflected by minimal bootstrap support for these clades. Clearly, greater representation and an in-depth intrageneric character analysis is required before proposing additional taxonomic modifications.

KEY TO THE GENERA OF OLIGOSITINI

1. Metasoma with terga uniformly sclerotized their entire length. Propodeal disk usually distinctly longer than metanotum at midline (Figs. 26–28). Propodeum and mesosomal pleural areas usually subrugulose (Figs. 27, 30). Mesopleuron with pleural suture (Fig. 30); transepisternal sulci absent (Fig. 32) (Oligositina) 2
- Metasoma with at least the three anterior terga longitudinally striate in posterior section, anterior section uniformly sclerotized (Figs. 29, 31). Propodeal disk usually only slightly longer than metanotum (Fig. 29). Propodeum and mesosomal pleural areas smooth (Figs. 29, 31). Mesopleuron without pleural suture (Fig. 31); transepisternal sulci present (Fig. 33) (Eteroligositina) 8
2. Fore wing disk entirely glabrous (rarely with one or two setae) (Fig. 2). Mesosoma with a small subtriangular lobe arising beneath propodeal disk (Fig. 25). Mesotarsus elongate, distinctly longer than mesotibia 3
- Fore wing disk sparsely to moderately densely setose (Figs. 3, 4). Mesosoma without a small subtriangular lobe arising beneath propodeum. Mesotarsus not longer than mesotibia 4
3. Antenna with a distinct funicular segment (Fig. 16) *Epoligosita (Epoligosita)*
- Antenna without a distinct funicular segment *Epoligosita (Epoligositina)*
4. Maxillary palps absent (Fig. 24). Antenna without linear placoid sensilla on surface of club (males unknown) *Sinepalpigramma*
- Maxillary palps present. Antenna with linear placoid sensilla on surface of last two segments of club 5
5. Antenna with four postanellar segments, including a single funicular segment distinctly separated from a three-segmented club (Fig. 18). Mesophragma notched apically. Many species with a clavate terminal process (= modified placoid sensilla) at apex of club in females (Fig. 19) *Oligosita*
- Antenna with three or four postanellar segments, if with four then the funicular segment closely associated with club (Fig. 20). Mesophragma not notched apically. Without a clavate terminal process on apex of club of females 6
6. Fore wing of moderate width, ca. 3× as long as wide (as in Fig. 3) *Prosoligosita*
- Fore wing extremely narrow, ca. 7× as long as wide (Fig. 4) 7
7. Antenna with three postanellar segments (Fig. 17). Fore wing sparsely setose with only one or two rows of setae on disk *Megaphragma*
- Antenna with four postanellar segments (Fig. 20). Fore wing densely setose (Fig. 4) *Prestwichia*
8. Antennal club one segmented 9
- Antennal club two or three segmented 10
9. Funicular segment longer than wide. Ovipositor elongate, extending well beyond apex of metasoma. Male genitalia with posteriorly directed apodemes at base (as in Fig. 12) *Chaetostrichella*
- Funicular segment wider than long. Ovipositor relatively short, not extending beyond apex of metasoma or only slightly so. Male genitalia without posteriorly directed apodemes (as in Fig. 11) *Doirania*
10. First club segment somewhat disassociated from segment II, appearing as a second funicular segment (Fig. 9). Fore wing densely setose (Fig. 6). Ovipositor extending well beyond apex of metasoma *Probrachista*
- First club segment closely appressed to second, distinct from funicular segment (Fig. 22).

- Fore wing variable but usually not densely setose (as in Figs. 5, 7). Ovipositor variable in length but rarely extending more than slightly beyond apex of metasoma 11
11. Ovipositor with 3rd valvulae bristlelike, abruptly narrower than 2nd valvulifer (inner plates). Last sternum of male extending posteriorly well beyond apex of last tergum (Fig. 39). Genitalia extremely long (Fig. 38), folded upon itself when not exerted (Fig. 39), strongly bifurcate apically (Fig. 38) 12
- Ovipositor with 3rd valvulae normal, not bristlelike, not abruptly narrower than 2nd valvulifer. Last sternum of male not extending beyond apex of last tergum (Fig. 13). Genitalia of normal length, only slightly bifurcate (Fig. 36) *Pseudoligosita*
12. Male antenna (Fig. 21) with placoid sensilla on all three club segments, those on C3 relatively narrow; funicular segment short, wider than long. Hind wing with three setal tracks *Hayatia*
- Male antenna (Fig. 8) without placoid sensilla on first club segment, second and third club segments with extremely wide placoid sensilla; funicular segment about as long as wide. Hind wing with two setal tracks *Eteroligosita*

Subtribe Oligositina Walker

Diagnosis: Antenna with funicle distinct from club or closely appressed to it. Fore wings relatively narrow to very narrow, with disk glabrous to moderately densely setose; stigma subcircular or suboval, usually sessile to marginal vein or connected by a slight constriction; dorsum and sides of mesosoma usually subrugulose; propodeal disk typically subtriangular or subrectangular, considerably longer than metanotum; pleural suture present on mesopleuron; mesosternum without transepisternal sulci. All metasomal terga uniformly sclerotized their entire length; metasomal tergum II (1st visible) often longitudinally rilled medially (Figs. 26, 27). Male genitalia simple, consisting of a single tubular structure and, at most, 2 anteriorly directed apodemes at base.

Epologosita Girault

Paroligosita Girault and Dodd, in Girault 1915: 145 (as subgenus of *Oligosita*). Type species: *Paroligosita biclavata* Girault and Dodd, by original designation.

Epologosita Girault 1916: 206 (n. n. for *Paroligosita* Girault and Dodd, nec Kurdjumov 1911) (as genus).

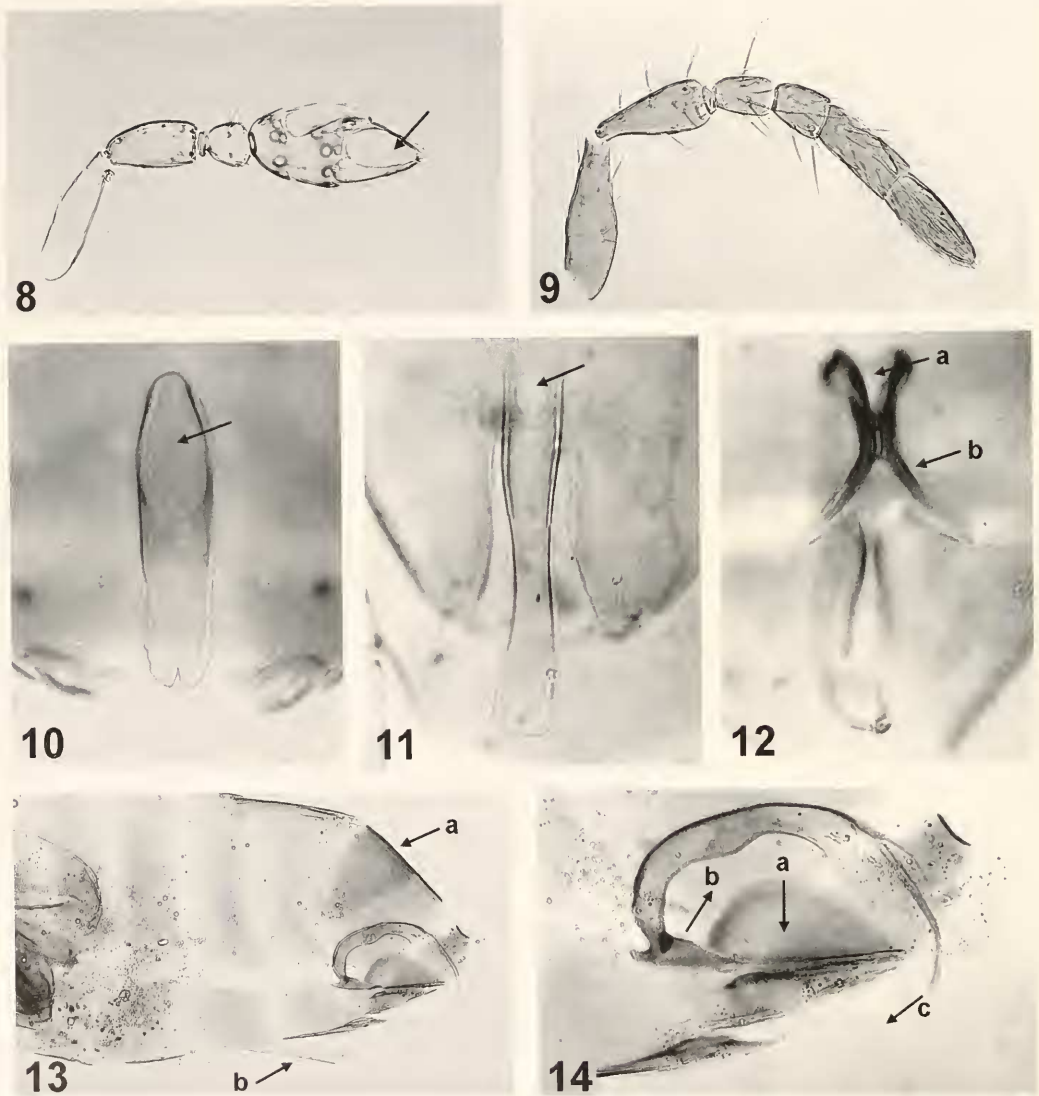
Epologositina Livingstone and Yacoob 1983: 214 (as subgenus). Type species: *Epologosita (Epologositina) duliniae* Livingstone and Yacoob,

by original designation. Lin 1990 (as genus).
Renewed status as subgenus.

Diagnosis.—Antenna with 1 funicular segment present or absent, and a 1–2 (rarely 3) segmented club; sutures subdividing club often incomplete; funicle, when present, distinct from club. Tarsi elongate, those of fore and middle leg longer than their respective tibia; tarsomere I of mesotarsus especially elongate in most species. Fore wing ca. 3–4× as long as wide, widest near level of stigma, gradually narrowing to apex; fringe setae elongate, length varying from subequal to wing width to ca. 2× greater; disk bare, with at most 1 or 2 setae; entire posterior margin evenly arcuate; premarginal vein abruptly wider than marginal vein at junction. Propodeal disk subtended by a small subtriangular lobe.

The shape of the fore wing (widest at the stigma, narrowing to apex), the virtual absence of setae on the fore wing disk, the presence of the triangular lobe subtending the propodeal disk, and the elongate tarsi provide the best separation of *Epologosita* from other genera.

Comments.—There are 22 described species of *Epologosita*. We recognize two subgenera, the nominate subgenus with 17 species and *Epologositina* with five. The for-



Figs. 8-14. 8-9, antennae. 8, *Eteroligosita* (medial; arrow to greatly enlarged placoid sensillum on last club segment). 9, *Probrachista*. 10-14, male genitalia. 10, *Uscana semifunipennis* Girault (dorsal; arrow to relatively large anterodorsal aperture). 11, *Oligosita* (dorsal; arrow to reduced anterodorsal aperture). 12, *Pseudoligosita* (ventral; arrow-a to reduced anterodorsal aperture, arrow-b to posteriorly directed apodemes at base of genitalia). 13, *Pseudoligosita* (lateral of metasoma; arrow-a to modified metasomal tergum VII above genitalia, arrow-b to medial projection of sternum IV beneath genitalia). 14, *Pseudoligosita* (as 13, higher magnification of genitalia and associated sterna). Arrows illustrate unique process of genitalia eversion: domed shape sternum VII is brought down and flattened (direction indicated by arrow-a); the flattening of sternum VII rocks base of genitalia forward (direction indicated by arrow-b) thus swinging the genitalia out of body and forward (direction indicated by arrow-c).

mer, although uncommonly collected, is known from all major regions of the world. *Epoligositina* occurs in Asia (India, China, Japan), and we have examined a

single female of an apparently consubgeneric species from Somalia.

Epoligositina was described as a subgenus of *Enoligosita* by Livingstone and Ya-

coob (1983), distinguished by the lack of a funicular segment and more extensive fumination in the fore wing. The group was elevated to genus by Lin (1990). Considering the variation in antennal segment number among obviously related species of Oligositini we do not feel separation at the generic level is warranted. Subgeneric status also could be questioned, but we believe it appropriate considering the limited material of *Epoligositina* available for this study.

As indicated, there is considerable variation in antennal formula in *Epoligosita*. In addition to the presence or absence of a funicle, club structure also varies. In most species the club is one or two segmented; in some it is incompletely two or three segmented; and in a male of an undescribed species from New Guinea (female unknown) it is clearly three segmented. Thus, in the New Guinea species the antennal formula is exactly the same as in *Oligosita* and many other oligositines (one distinct funicular segment, three segmented club). This suggests that reduction in segmentation occurred after the origin of the genus.

Both subgenera of *Epoligosita* are known to attack eggs of Cicadellidae (Livingstone and Yacooob 1983, Viggiani 1985, Pinto and Viggiani 1987).

Material from throughout the range of *Epoligosita* (*Epoligosita*) was examined. Only two specimens representing two species of *E.* (*Epoligositina*) were available.

Megaphragma Timberlake

Megaphragma Timberlake 1923: 412. Type species: *Megaphragma mymaripenne* Timberlake, by original designation.

Sethosiella Kryger 1932: 38. Type species: *Sethosiella priesneri* Kryger, by original designation.

Paramegaphragma Lin 1992: 133. Type species: *Paramegaphragma stenopterum* Lin, by original designation.

Diagnosis.—Extremely small, body length less than 0.3 mm. Antenna with

0–1 funicular segments and 2–3 club segments; if funicle present, club with 2 segments; if funicle absent, club with 2 or 3 segments. Fore wing extremely narrow, strapshaped, ca. 7× as long as wide, with retinacular margin distinctly arcuate; fringe setal length ca. 5× greatest wing width; number of setae on disk few, varying from 0 to several arranged in 1 or 2 setal lines.

The minute body size (< 0.3 mm), and the exceptionally narrow, sparsely setose fore wing with its extremely long fringe setae separate *Megaphragma* from all other Oligositina.

Comments.—*Megaphragma* includes 15 species. Of the synonyms, *Sethosiella* was described by Kryger (1932) without any indication that he was aware of Timberlake's earlier description of *Megaphragma*. *Paramegaphragma* was described by Lin (1992) for species without a funicle and only two club segments. Its synonymy was proposed by Delvare (1993).

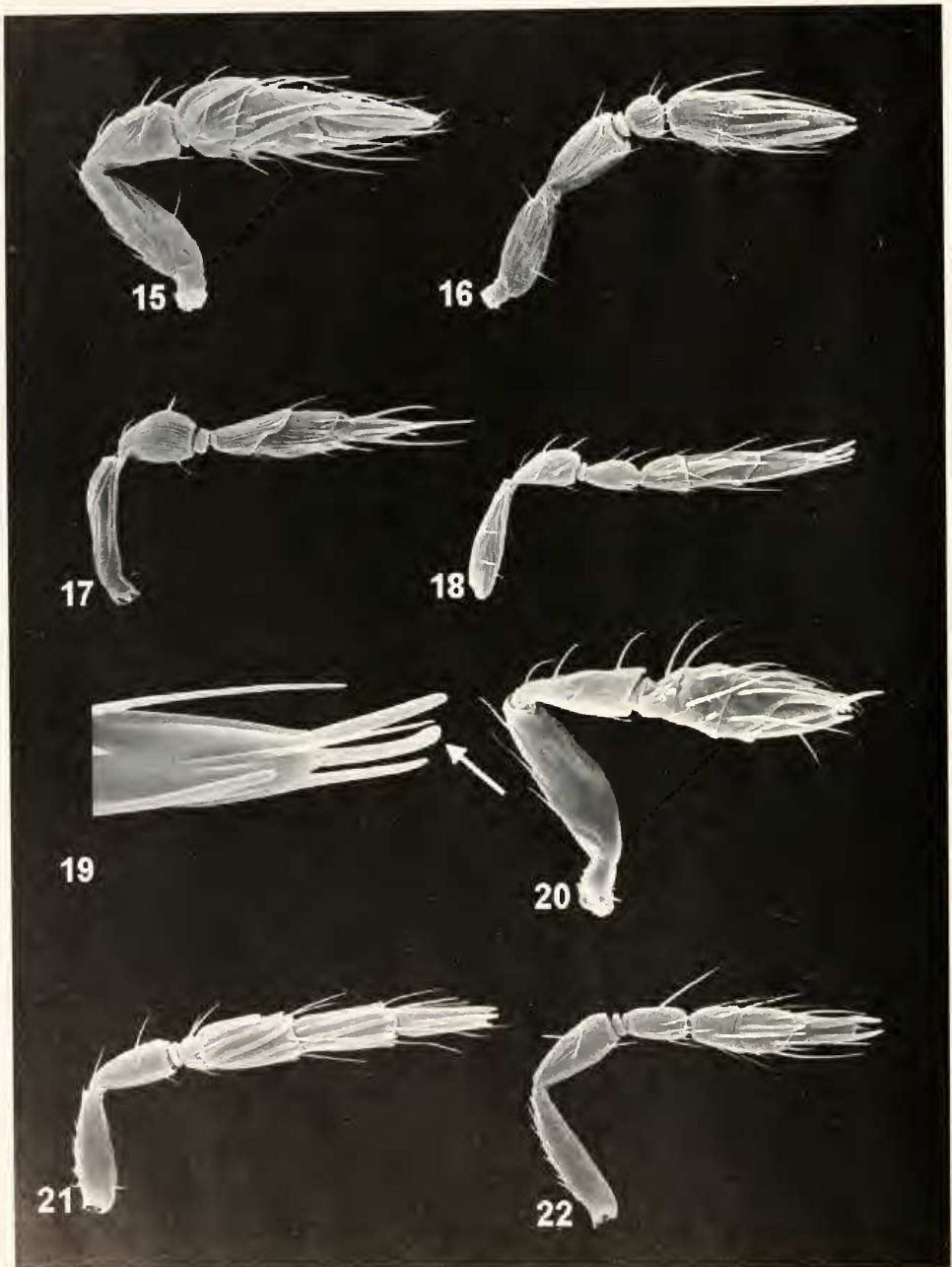
The species can be divided into three informal groups: (a) those with a funicle and a two-segmented club (*mymaripenne*, *amalphitanum* Viggiani, *decohaetum* Lin, *polychaetum* Lin, *maguiclava* Yousuf and Shafee, *longiciliatum* Subba Rao, *priesneri*, and *anomalifuniculi* Yuan and Lou); (b) those without a funicle and a three-segmented club (*striatum* Viggiani, *aligarhensis* Yousuf and Shafee, and *ghesquierei* Nowicki); and (c) those without a funicle and a two-segmented club (*caribea* Delvare, *macrostigmum* Lin and *stenopterum* Lin). A revisionary study is required to determine if these represent natural groups.

Megaphragma is known from all biogeographic regions. Thysanoptera eggs are commonly recorded as hosts (Lin 1994).

We have examined several species of *Megaphragma* from all regions, including representatives of the three informal groups indicated.

Prestwichia Lubbock

Prestwichia Lubbock 1864: 140. Type species: *Prestwichia aquatica* Lubbock, by monotypy.



Figs. 15–22. Antennae. 15, *Uscaua semifumipennis* (lateral, ♀). 16, *Epoligosita* (lateral, ♀). 17, *Megaphragma striatus* (lateral, ♀). 18, *Oligosita* (Collina Group) (medial, ♀). 19, same as Fig. 18, detail (arrow to clavate placoid sensillum at apex of club). 20, *Prestwichia* (lateral, ♀). 21, *Hayatia* (medial, ♂). 22, *Pseudoligosita* (lateral, ♀).

Austromicron Tillyard 1926: 279. Type species: *Austromicron zygopterorum* Tillyard, by original designation.

Diagnosis. Antenna with 1 funicular segment and 3 club segments; funicular segment closely associated with club. Mesosoma with dorsal surface distinctly reticulate. Propodeal disk distinct, elongate, subtrapezoidal. Fore wing very narrow, rounded apically, ca. 7× as long as wide; fringe setae 2.5–3× greatest wing width; retinacular margin moderately arcuate; disk densely setose at apical half. First tergum of metasoma with a rhomboidal-shaped platform at center. Males often wingless.

The characteristics of the fore wing (extremely narrow but densely setose), the close association of the funicle with the club, and absence of apical metasomal spiracles separate this genus from all other Oligositina. The rhomboidal-shaped platform at the center of the first visible metasomal tergum (Fig. 28) may be another distinguishing feature but its presence has not been verified in all species.

Comments.—*Prestwichia* includes five described species. The Australian *P. zygopterorum* was placed in its own genus (*Austromicron*) by Tillyard (1926) based on relatively minor traits, including fully alate males and a shorter, non-protruded ovipositor. The synonymy was recognized by Doutt and Viggiani (1968).

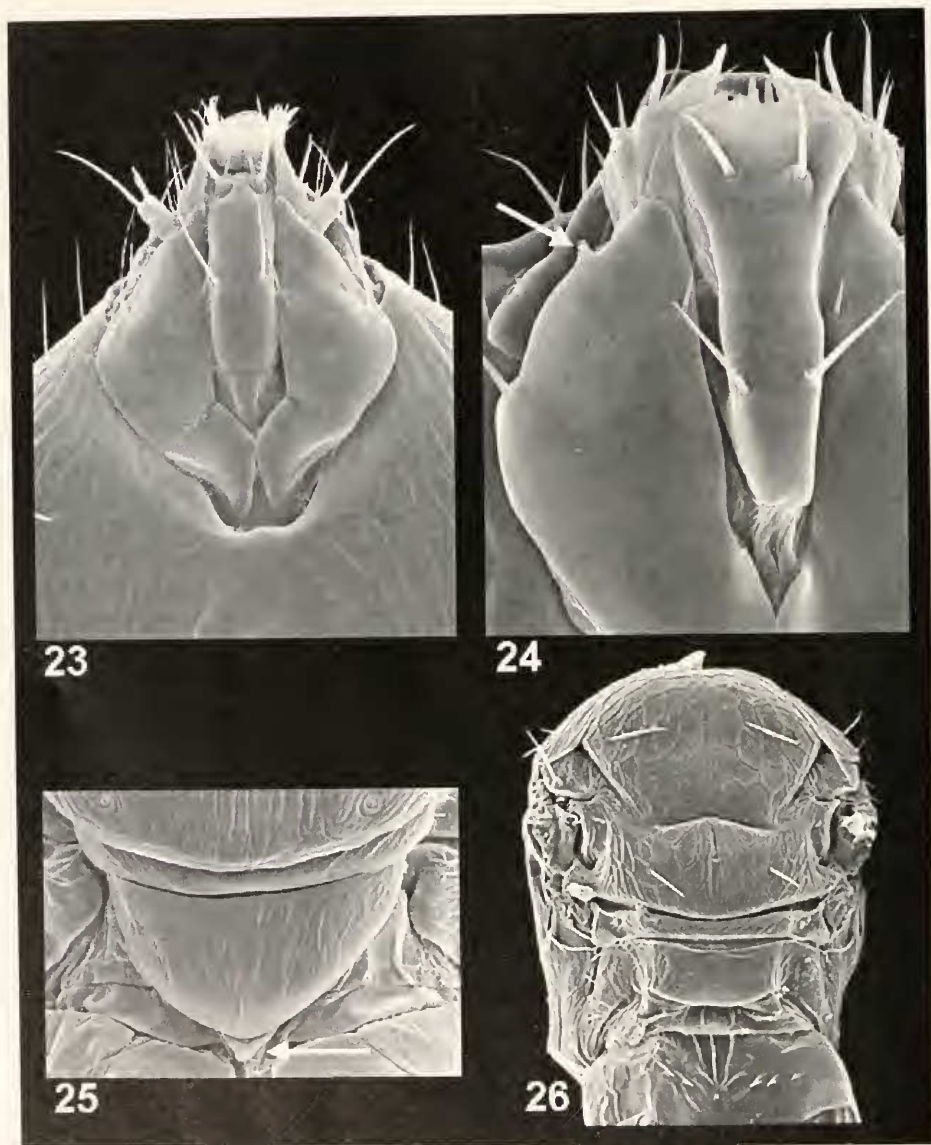
Described species of this uncommonly collected genus occur in Europe, Asia and Australia. It also has been collected from Africa (Ivory Coast) and North America (Florida) (unpubl.). It has yet to be taken in the Neotropics. *Prestwichia* has been recorded parasitizing eggs of a variety of aquatic Coleoptera, Hemiptera, and Odonata (Fursov 1995). We have examined described (*P. aquatica*, *P. zygopterorum*) and undescribed species from all areas of distribution.

Prosoligosita Hayat and Husain

Prosoligosita Hayat and Husain 1981: 81. Type species: *Prosoligosita perplexa* Hayat and Husain 1981, by original designation.

Diagnosis.—Antenna with a 4-segmented club; a distinct funicle absent; C4 longest of club segments and extremely narrow in female (> 3× as long as wide), C2 the shortest; placoid sensilla present on C1, C3 and C4 in both sexes, absent from C2 (i.e., from 2nd postanellar segment as in all oligositines). Fore wing almost 3× as long as wide; fringe setae almost as long to somewhat longer than maximum wing width (but not as long as twice maximum width); retinacular margin distinctly arcuate relative to remainder of posterior wing margin; stigma constricted at junction with marginal vein; disk sparsely setose with setae arranged in ca. 7 well-separated lines. The apparently 4-segmented club combined with the elongate and exceptionally narrow last club segment in females, the presence of a linear placoid sensillum on the 1st postanellar antennal segment, and the occurrence of apical metasomal spiracles separate *Prosoligosita* from other members of its subtribe.

Comments.—*Prosoligosita* was described from three females of a single species from India. A second Indian species, *P. meerutensis*, described by Yousuf and Shafee (1993) is known only from its unique type female. The only material of this genus discovered since these original descriptions includes a single male from Bangalore, India, a female from Sarawak, and a second female from Sulawesi. These three specimens are the only ones we have examined of this genus. The male is likely conspecific to *P. perplexa*; the females cannot confidently be placed to species but appear to be different yet close to *P. perplexa*. The male of *Prosoligosita* was not known previously. Its antennal features are similar to those of the female except the terminal club segment is not as elon-



Figs. 23–26. 23–24, ventral of head showing maxillae. 23, *Oligosita* (with 1-segmented maxillary palps). 24, *Sinepalpigramma longiciliatum* (arrow to appendicular remnant of maxillary palp). 25, *Epilogosita*, propodeal disk (arrow to subpropodeal lobe). 26, *Oligosita* (Minima Group), mesosoma and base of metasoma (dorsal).

gate (ca. 2× as long as wide); the genitalia are typical for the Oligositina.

The distinct four-segmented club appears to render this genus unique in the Oligositini. However in *Prestwichia* and *Sinepalpigramma*, the funicular segment closely approaches the club; it is only somewhat more closely appressed to the

apical three flagellar segments in *Prosoli-gosita*, a minor difference at best. *Prosoli-gosita* also is distinguished by the presence of a linear placoid sensillum on the first postanellar segment in both sexes (= C1 in this genus). The only other occurrence of this trait in the tribe that we are aware of is in a few species of apparently unde-

scribed Australian *Oligosita* which have a linear placoid on the funicular segment.

Sinepalpigramma Viggiani and Pinto

Sinepalpigramma Viggiani and Pinto (2003). Type species: *Sinepalpigramma longiciliatum* Viggiani and Pinto, by original designation (type examined).

Diagnosis.—Antenna with a single funicular segment and a 3-segmented club; funicle closely associated with 1st club segment; antenna completely without linear placoid sensilla on surface and with only a single type of seta-like structure on flagellum. Females without maxillary palps. Surface of mesoscutum and scutellum extremely smooth, without any indication of reticulae.

Sinepalpigramma is perhaps the most easily recognized genus of Oligositini. The absence of maxillary palps is unique in the family. Antennal structure, the absence of antennal placoid sensilla, and the smooth mesosomal dorsum also are distinctive for the tribe.

Comments.—A clear male association is unknown. A single, poorly prepared male from Costa Rica may belong here. Character 29 (features of male genitalia) was coded for *Sinepalpigramma* based on this male. There are two described species. The genus occurs from central Mexico south to Argentina. Hosts are unknown.

Oligosita Walker

Oligosita Walker 1851: 212. Type species: *Oligosita collina* Walker, by monotypy.

Westwoodella Ashmead 1904: 359. Type species: *Oligosita subfasciata* Westwood, by original designation. Syntypes examined.

Paroligosita Kurdjumov 1911: 434. Type species: *Paroligosita bella* Kurdjumov, by original designation.

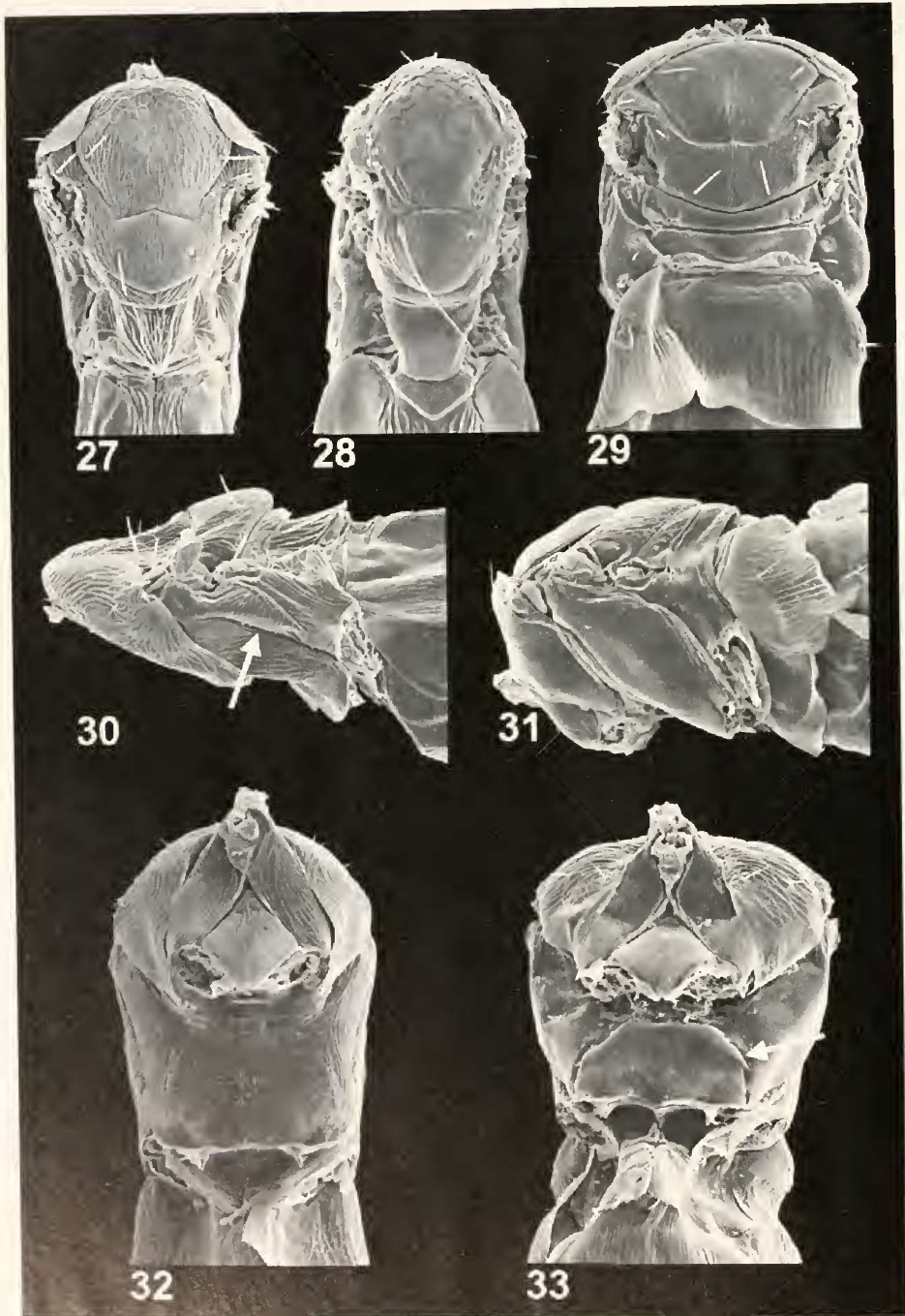
Diagnosis.—Antenna with funicle distinctly separated from 3-segmented club. Maxillary palps present. Fore wing sparsely to moderately densely setose, no more than ca. 4× as long as wide. Propodeal

disk not subtended by a small subtriangular lobe.

Antennal structure alone separates *Oligosita* from virtually all other Oligositina. *Megaphragma* and most *Epoligosita* have fewer segments, and *Prestwichia*, *Prosoligosita* and *Sinepalpigramma* appear to have a 4-segmented club. Any *Epoligosita* with similar antennal structure can be separated by wing and propodeal features. The presence of maxillary palps also separates *Oligosita* from *Sinepalpigramma*.

Comments.—Several species are removed from *Oligosita* and placed in *Pseudoligosita* (see below); approximately 95 species remain assigned. It is likely that further partitioning will be necessary when the group is better known. The lack of clear-cut synapomorphic traits for assemblages other than the Collina Group preclude additional revision at the present time.

Oligosita, as defined here, is readily identifiable but remains paraphyletic and possibly polyphyletic (Fig. 1). For purposes of phylogenetic analysis we divided it into three broad assemblages, as already indicated. The Collina Group (= *Oligosita*-C in Fig. 1), the largest assemblage, almost certainly is monophyletic. In this group, females have a characteristic clavate apical placoid sensillum forming a terminal process on the antennal club (Fig. 19). The group is distinguished further by the structure of the fore wing venation. In most oligositines the premarginal vein does not deviate greatly from the marginal vein but remains close to the anterior margin of the wing. In the Collina Group, the premarginal diverges posteriorly from the marginal vein leaving a distinct costal cell. A further distinction is the placement of the presumed apical premarginal seta in the costal cell rather than on the premarginal vein itself as occurs in most oligositines having two premarginal setae. Most known species of the Collina Group also have a distinctly triangular propodeal disk (Fig. 27).



Figs. 27–33. Mesosoma and base of metasoma. 27–29, dorsal. 27, *Oligosita sanguinea* (Girault) (Collina Group). 28, *Prestwichia*. 29, *Pseudoligosita* (note striate posterior section of metasomal tergum). 30–31, lateral. 30, *Oligosita sanguinea* (arrow to mesopleural suture). 31, *Pseudoligosita*. 32–33, ventral. 32, *Oligosita*. 33, *Pseudoligosita* (arrow to transepisternal sulcus).

The Minima Group (= *Oligosita*-M in Fig. 1) is separated from other *Oligosita* by the arcuate retinacular margin of the fore wing, the single campaniform sensillum at the apex of the premarginal vein and absence of an apical premarginal seta. These traits also occur in other genera of the subtribe and the group may not be monophyletic.

Additional *Oligosita* included here are generalized species which, as a group, do not vary in the characters used for analysis. They were represented in the phylogenetic analysis by a single undescribed species from Western Australia (= *Oligosita*-G in Fig. 1). Their relationship to one another, and to other representatives is unknown. They are retained in *Oligosita* until the genus is better understood.

The Walker type of *O. collina*, the type species, originally from the Haliday Collection, could not be located. It is not deposited in The Natural History Museum (London), The Hope Department of Entomology (Oxford University), or the National Museum of Ireland. Portions of the Haliday collection were widely dispersed to many other museums (O'Connor and Nash 1982) and there is no basis at this time to consider the type lost. We follow the traditional definition of *O. collina* in this paper which defines it as having a clavate sensillum at the apex of the female antenna (Nowicki 1936, Viggiani 1976b) (= Collina Group).

The female types of the type species of *Westwoodella*, *O. subfasciata* Westwood, were examined and are assignable to the Collina Group. The clavate sensillum at the antennal apex, the triangular propodeal disk, and fore wing characteristics clearly place it here. Certain workers (Nowicki 1936, Viggiani 1976b), assuming the absence of the characteristic clavate sensillum in *O. subfasciata*, related the species with an entirely distinct group which we, in part, treat as *Pseudoligosita* (see below). Inconsistencies exist between the types of *O. subfasciata* and the original de-

scription of *Westwoodella*. Ashmead (1904) characterizes *Westwoodella* as having a bicarinate metanotum and its funicle as much longer than wide. Neither feature characterizes *O. subfasciata*. The funicle is only slightly longer than wide, and we assume that the 'bicarinate metanotum' refers to the propodeal disk which Westwood (1879) indicates in his drawing of *O. subfasciata* by two subparallel lines.

The types of *Paroligosita bella* are in the Zoological Museum in St. Petersburg. Two of several syntypes were examined. Kurdjumov (1911) considered *P. bella* close to *O. collina* and his description is consistent with certain European species belonging to the Collina Group. The syntypes confirm this.

We examined *Oligosita* from throughout its range. This included over 30 species plus numerous undescribed species. Most species of *Oligosita* parasitize eggs of auchenorrhynchous Hemiptera, particularly Cicadellidae (see Viggiani 1982a, Lin 1994).

Subtribe Eteroligositina Lin, **new status**

Eteroligositini Lin, 1993

Diagnosis.—Antenna with funicle always distinct from club. Fore wings moderately broad, moderately to densely setose; stigma rectangular or subtriangular in shape, usually with a distinct constriction between stigma and marginal vein; mesosoma relatively smooth laterally, obsolescently reticulate dorsally; propodeal disk straplike or only slightly produced posteriorly, not considerably longer than metanotum; pleural suture absent; mesosternum with transepisternal sulci. Mesosoma with anterior terga divided into an anterior uniformly sclerotized portion, and a posterior, longitudinally striate section; surface of 1st visible tergum never longitudinally rilled medially. Male genitalia varying in structure.

Comments.—Lin (1993) defined the Eteroligositini to include *Eteroligosita* and *Hay-*

atia based on their distinctive male genitalia. We are returning these genera to the Oligositini but use Lin's family group name as a subtribe.

Based on the examination of several species, any *Oligosita* with longitudinally striate metasomal terga should be transferred to the Eteroligositina. Thus far, we have found that this feature always is correlated with the other mesosomal traits characterizing this subtribe. We are aware of only a single species that remains somewhat questionable as to subtribal assignment. This is *Pseudoligosita gerlingi* (Viggiani). Wing and male genitalic morphology is as in Oligositina. The propodeum, the longitudinally striate metasomal terga, and the relatively smooth mesosomal surfaces place it in Eteroligositina. The two specimens available on slides also suggest the absence of the pleural suture on the mesothoracic segment. This species may represent a basal lineage of Eteroligositina.

Doirania Waterson

Doirania Waterston 1928: 386. Type species: *Doirania leafmansii* Waterson 1928, by original designation. Types examined.

Diagnosis.—Antenna with a single club segment, and a transverse funicular segment. Foramen magnum in a more dorsal position than in other oligositines. Male with a single ventromedial projection on sternum and genitalia similar to that in Oligositina (reduced to a tube with 2 short apodemes at base).

Comments. *Doirania* was recently reviewed by Pinto (2004). The genus, known from North America, the Palearctic and New Guinea, currently includes three species. A few species that currently key to *Pseudoligosita* probably belong here. They have a three segmented club, but other features, namely the short, transverse funicle, and dorsal position of the foramen magnum, suggest *Doirania*. Males are unknown. Because of the considerable differ-

ences in genitalic structure between *Doirania* and *Pseudoligosita*, generic placement remains questionable. All described species were available for study.

Pseudoligosita Girault

Pseudoligosita Girault 1913: 104. Type species: *Pseudoligosita arnoldi* Girault, by original designation (type examined). **Renewed status**. *Zorontogramma* Silvestri 1915: 104. Type species: *Zorontogramma distinctum* Silvestri, by original designation (types examined). Doutt and Viggiani 1968: 537 (as subgenus of *Oligosita*). *Oligosita*: Viggiani 1976b: 188 (Arnoldi and Subfasciata groups, in part).

Diagnosis.—Antenna with 2 or 3 club segments; funicular segment usually as long as wide or distinctly longer than wide; linear placoid sensilla normal in width and absent from C1 in species with a 3-segmented club. Fore wing moderately to, rarely, densely setose; setae usually not uniformly distributed on apical half of disk. Hind wing almost always with 2 lines of setae on disk. Ovipositor short to moderately long, rarely surpassing apex of metasoma; third valvula of normal width, never bristlelike. Metasomal venter of male usually with a single elongate, spathulate, sternal projection. Male genitalia of most species with posteriorly directed apodemes at base; genitalia strongly curved ventrally; last sternum not extending beyond apex of last tergum.

The 2–3 segmented club in combination with the relatively short ovipositor (not extending beyond apex of metasoma) separate *Pseudoligosita* from all eteroligositine genera except *Hayatia* and *Eteroligosita*. From these taxa, females are separated by the normal, non-bristlelike, third valvula. Males are easily distinguished by the last metasomal sternum which does not extend beyond the apex of the last tergum.

Comments.—Several species described as *Oligosita* must be transferred to *Pseudoligosita*. Reassignment is based on examination of types or authoritatively identified material and/or clear evidence in-

dedicated in the original descriptions. Species referable to *Pseudoligosita* (**new combinations**) include the following: *acuticlavata* Lin, *aesopi* Girault, *anima* Girault, *arnoldi* Girault (type species), *brevicilia* Girault, *comosipennis* Girault, *curvata* Lin, *distincta* Silvestri (type species of *Zorontogramma*), *dolichosiphonia* Lin, *elimiae* Viggiani, *elongata* Lin, *fasciata* Viggiani, *fasciati-pennis* Girault, *funiculata* Girault, *fuscipennis* Girault, *gerlingi* Viggiani, *gracilior* Novicky, *grandiocella* Lin, *gutenbergi* Girault, *idioceri* Viggiani, *inermiclava* Girault, *krygeri* Girault, *kusaiensis* Doutt, *longiclavata* Viggiani, *longicornis* Lin, *longifrangata* Viggiani, *lutulenta* Novicky, *marilandia* Girault, *nephotetticum* Mani, *nigripes* Girault, *nowickii* Viggiani, *numiciae* Viggiani, *paphlagonica* Novicky, *plebeia* Perkins, *podolica* Novicky, *phanopterae* Viggiani, *platyoptera* Lin, *robusta* Viggiani, *schlicki* Kryger, *servadeii* Viggiani, *tachikawai* Yashiro, *transverscutata* Lin, *tumidiclava* Viggiani, *utilis* Kowalski, *xiphidii* Ferrière, *yasumatsui* Viggiani and Subba Rao. Certain species remaining in *Oligosita* probably will require reassignment when studied adequately.

Pseudoligosita probably is paraphyletic (Fig. 1). Its relationship to *Chaetostrichella* and *Probrachista* is unclear but it is possible that the latter two are derived from *Pseudoligosita*. *Pseudoligosita platyoptera* and *P. dolichosiphonia*, two Chinese species, approach *Probrachista*. Both have densely setose fore wings (as in Fig. 6), and *P. dolichosiphonia* also has a strongly exerted ovipositor (see Lin 1994).

Tentatively placed in *Pseudoligosita* are a few species whose males lack metasomal sternal modifications and distinctly curved genitalia (represented in the analysis by *Pseudoligosita*-I but also including *P. gerlingi* and *P. phanopterae*). Because these species possess features defining the Eteroligositina but none of the generic synapomorphies, they may represent basal subtribal lineages.

The type specimen of *Pseudoligosita arnoldi*, deposited in the Queensland Muse-

um, was examined. Girault (1913) separated *Pseudoligosita* from *Oligosita* by its shorter fore wing fringe, not by any of the features noted here.

Pseudoligosita is cosmopolitan in distribution. Although known to parasitize auchenorrhynchous Hemiptera as do other oligositine genera, several species have been associated with eggs of Orthoptera (Tettigoniidae) and Coleoptera (Chrysomelidae: Hispinae) (see Lin 1993).

Chaetostrichella Girault

Brachystira: Mayr 1904: 590.

Chaetostrichella Girault 1914: 147. Type species:

Chaetostrichella platoni Girault, by monotypy.

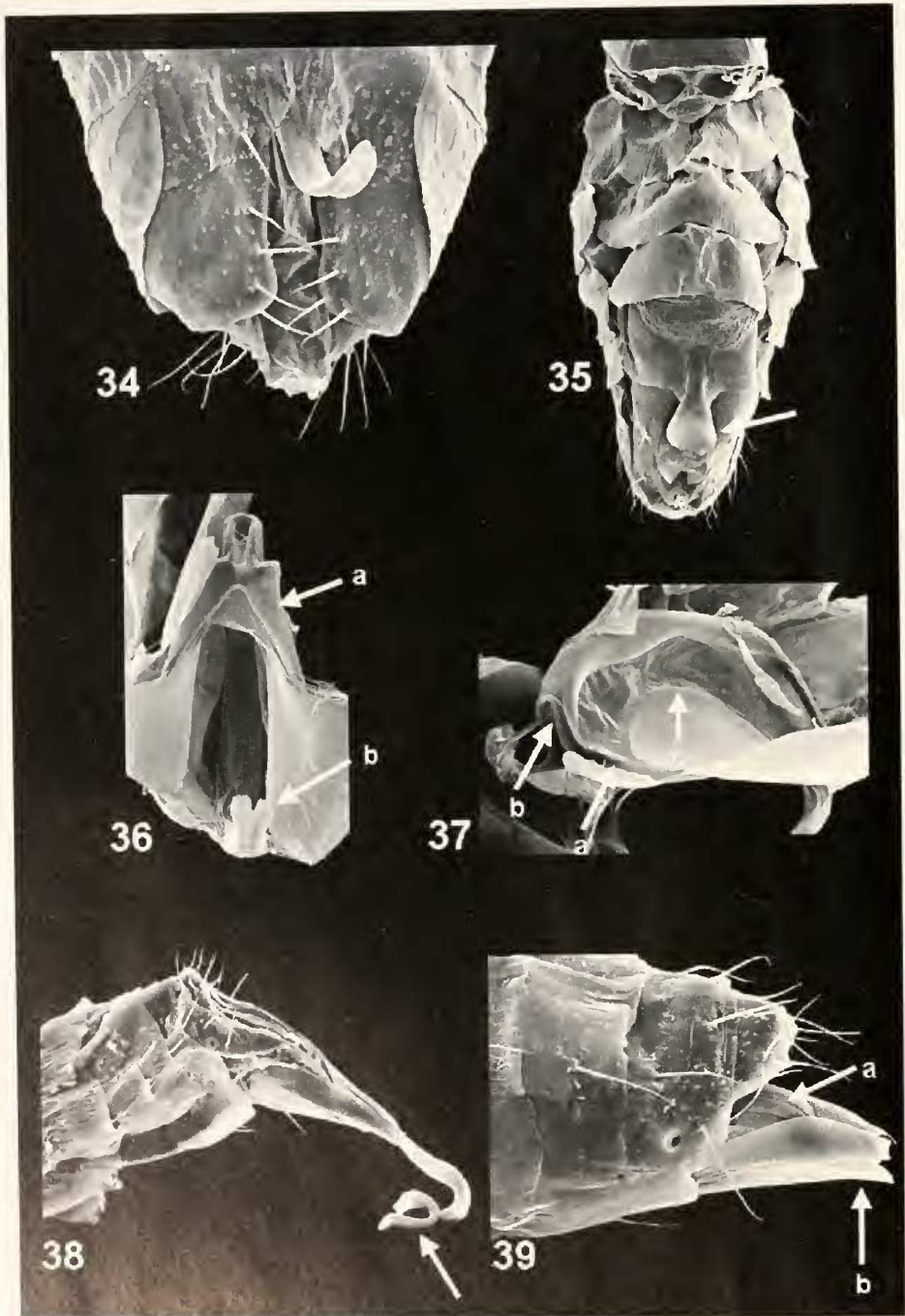
Pinto, 1993: 299 (renewed status).

Brachista: Nowicki 1936: 136. Doutt and Viggiani 1968: 497.

Diagnosis.—As in *Pseudoligosita* except as follows: Antennae with a 1-segmented club (which may be incompletely segmented in some specimens). Fore wing disk beyond level of venation densely, evenly setose; setae not arranged in vein tracks. Hind wing with 2 lines of setae on disk. Ovipositor very long, twice as long or longer than hind tibia, extending well beyond apex of metasoma.

Features separating *Chaetostrichella* from *Pseudoligosita* also separate it from *Doirania*, the other Eteroligositina genus with a single club segment. It also is distinguished from *Doirania* by the elongate funicular segment (transverse in *Doirania*) and male genitalia which, as in *Pseudoligosita*, have 2 strong posteriorly projecting apodemes at the base. The elongate ovipositor and densely setose fore wing also characterize *Probrachista*. However *Chaetostrichella* is easily separated by its 1-segmented club (3-segmented in *Probrachista*).

Comments.—*Chaetostrichella* includes three Palaearctic species (Nowicki 1936, Doutt and Viggiani 1968) which historically were erroneously associated with *Brachista* (see Pinto 1993). It is similar to *Pseudoligosita* and, with *Probrachista*, may represent a derived lineage of that genus.



Figs. 34–39. Male genitalic structures. 34, *Oligosita* (genitalia exserted between divided last sternum). 35, *Pseudoligosita* (venter, arrow to posterior projection of sternum IV). 36, *Pseudoligosita* [ventral, anterior = up; sterna peeled away to expose genitalia; arrow-a to posteriorly directed apodemes at base of genitalia (note anterodorsal aperture immediately anterior), arrow-b to bifid genitalic apex]. 37, *Pseudoligosita* [lateral of genitalia and associated sternal complex; arrow-a to posteriorly directed apodeme which is attached to anterior border of sternum VII; arrow-b to anterodorsal aperture (note ejaculatory duct entering aperture); arrow-c to roof of sternum VII (also see Fig. 14)]. 38, *Hayatia* (lateral, arrow to bifid apex of exserted genitalia). 39, *Hayatia*

Hosts are unknown. Limited collection data suggest that species are associated with aquatic habitats. Our treatment of this genus is based on the study of several unidentified females from Italy and an unidentified male from Kyrgyzstan.

Probrachista Viggiani

Probrachista Viggiani 1968: 521 (in Doutt and Viggiani 1968). Type species *Probrachista nepalensis* Viggiani, by original designation (type examined).

Diagnosis.—Female as in *Chaetostrichella* except as follows: Antenna with a 3-segmented club; 1st club segment loosely associated with C2 and C3, and appearing somewhat as a second funicular segment. Hind wing with 3 complete lines of setae on disk (1 dorsal, 2 ventral). Ovipositor extremely long, greater than twice as long as hind tibia, extending well beyond apex of metasoma; unique for oligositines in that the curved ramus edge of the semi-circular sheets are positioned considerably anterior to the gonangulae. Male unknown.

Antennal structure and the 3 setal tracks on the hind wing separates *Probrachista* from *Pseudoligosita*. In addition, the strongly exerted ovipositor, and the evenly, densely setose fore wing disk separates it from virtually all members of that genus (see above for exceptions).

Comments.—*Probrachista* was characterized by Viggiani (1968) as having two funicular and two club segments; the above diagnosis indicates a one-segmented funicle and a three segmented club. Distinguishing between funicle and club segments often is subjective, and this certainly is the case with *Probrachista*. The first club segment is slightly less intimately associated with the second than the latter is with the third. Yet, it is not as distinct from these segments as it is from the funicular segment. For this reason, and so as to not imply a greater difference from other oligositines than is warranted, the club is treated as three segmented.

Only the type species from Nepal is assigned to *Probrachista*. Besides the type series we are aware of two additional specimens (from South Africa and Guinea). Additional material is needed to determine if these are conspecific to one another or to *P. nepalensis*.

As indicated above, *Probrachista* could not be included in the phylogenetic analysis. The overall similarity of females to those of *Chaetostrichella* suggests relationship. Together these genera may represent a derived lineage of *Pseudoligosita*.

Hayatia Viggiani

Hayatia Viggiani 1982b: 27. Type species: *Hayatia indica* Viggiani, by original designation (type examined). Viggiani 1996: 29.

Diagnosis.—Antenna with a single funicular segment and a 3-segmented club. Fore wings moderately broad, ca. 2.5× as long as wide, fringe setae 0.3–0.5 wing width. Hind wing with 3 rows of setae (a central track dorsally and an anterior and posterior track ventrally). Female with 3rd valvula abruptly narrower than 2nd valvifer, bristlelike (see Viggiani 1996). Male with funicular segment shorter than in female; antennal club of male elongate with numerous prominent, linear placoid sensilla on all 3 segments. Metasomal sterna with at least 2 medial prolongations; last sternum of metasoma extending further posteriorly than last tergum. Genitalia extremely elongate, bifid apically, folded on itself when not exerted (see Viggiani 1982b).

Males of *Hayatia* can be confused with no other genus of Oligositini. They are unique in having prominent linear placoid sensilla on all 3 segments of the elongate club. Their unique genitalic structure is shared with *Eteroligosita*. Females of *Hayatia* should be separable from those of *Eteroligosita* by the 3 setal tracks on the hind wing.

Comments.—Five species of *Hayatia* are described from the Ethiopian and Oriental

regions and from Cyprus (Viggiani 1996). The placement of *Paruscanoidea longiclavata* Yousuf and Shafee in *Hayatia* (Yousuf and Shafee 1988) is incorrect. For this study we examined the type species and at least one additional unidentified species.

Hayatia is a close relative of *Eteroligosita* and may eventually prove congeneric. However, because of the considerable difference in male antennal structure we retain generic status.

Eteroligosita Viggiani

Eteroligosita Viggiani 1976a: 265. Type species: *Eteroligosita tamaricis* Viggiani, by original designation (type examined).

Diagnosis.—Similar to *Hayatia* except male antennae without placoid sensilla on first club segment and with enormously enlarged placoid sensilla on the 2nd and 3rd club segment (each ca. $\frac{2}{3}$ width of segment). Also, hind wing with only an anterior and middle setal track.

Comments.—The male genitalia in *Eteroligosita* are similar to those in *Hayatia*. The type species was described from Israel; two additional species have been described from China (Lin 1994). *E. tamaricis* was retrieved from galls on *Tamarix* caused by *Amblypalpis olivierella* Ragusa (Gelechiidae). In addition to the type species, we have examined an unidentified species from South Africa (Mooketsi) reared from eggs of *Oxyrhachis rufula* Caper (Membracidae).

ACKNOWLEDGMENTS

This study was supported by grant 2001-35316-11012 from the USDA (NRICGP) (John D. Pinto, PI) and NSF PEET grant BSR-9978150 (John M. Heraty, PI). Gary Platner was responsible for the scanning electron microscope photography and plate preparation. We also are grateful to Chris Burwell (Queensland Museum), Norma Diaz and Marta Loíacono (Museo de la Plata), John Noyes (The Natural History Museum), Chris O'Toole (Oxford University) and Michael Shauff (National Museum of Natural History) for making type material available. Lin Nai-quan (Fujian Agriculture and Forestry University) also sent us type material for examination, and Serue-

Triapitsyn secured types of *Paroligosita bella* for examination.

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